Research Article



Barred Owl Occupancy Surveys Within the Range of the Northern Spotted Owl

J. DAVID WIENS,¹ Department of Fisheries and Wildlife, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR 97331, USA

ROBERT G. ANTHONY, Department of Fisheries and Wildlife, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR 97331, USA

ERIC D. FORSMAN, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corvallis, OR 97331, USA

ABSTRACT The range expansion by barred owls (Strix varia) into western North America has raised considerable concern regarding their potential effects on declining northern spotted owl (Strix occidentalis caurina) populations, yet most information on the occurrence of barred owls in the region is limited to incidental detections during surveys for spotted owls. To address this shortcoming we investigated response behavior, detection probabilities, and landscape occupancy patterns of barred owls in western Oregon, USA, during conspecific versus spotted owl call-broadcast surveys. Subtle differences in barred owl response behavior to conspecific versus spotted owl vocalizations combined with minor procedural differences between species-specific survey protocols led to a sizeable difference in estimated detection probabilities during conspecific (0.66, 95% CI = 0.61-0.71) versus spotted owl (0.48, 95% CI = 0.39-0.56) surveys. We identified 61 territorial pairs of barred owls during repeated surveys of a multi-ownership study area with the probability of occupancy being highest in the structurally diverse mixture of mature and old forests that occurred almost entirely on public lands. Our findings suggest that research and management strategies to address potential competitive interactions between spotted owls and barred owls will require carefully designed, species-specific survey methods that account for erratic response behaviors and imperfect detection of both species. Our sampling methods can be used by forest managers to determine the occurrence and distribution of barred owls with high confidence. © 2011 The Wildlife Society.

KEY WORDS barred owl, detection probability, northern spotted owl, occupancy modeling, Oregon, *Strix occidentalis caurina*, *Strix varia*.

The range expansion by barred owls (Strix varia) into western North America has raised considerable concern regarding their potential effect on native wildlife, especially the threatened northern spotted owl (Strix occidentalis caurina; Buchanan et al. 2007, Gutiérrez et al. 2007). As barred owls have rapidly increased their numbers throughout the range of the spotted owl, mounting evidence indicates that they are displacing, hybridizing with, and even killing spotted owls (Leskiw and Gutiérrez 1998, Kelly et al. 2003, Olson et al. 2005). Indeed, range-wide demographic analyses have shown that spotted owl populations have declined by 20-50% in areas where barred owls are most abundant and have been present the longest (Anthony et al. 2006). Despite the importance of this emergent threat to recovery efforts for spotted owls, nearly all information on the presence of barred owls where they are sympatric with spotted owls is limited to incidental detections recorded during surveys for spotted owls (Anthony et al. 2006, Gutiérrez et al. 2007, Livezey and Flemming 2007). Barred owls often respond aggressively to spotted owl calls (Dunbar et al. 1991, Crozier et al. 2006), but the probability of detecting barred owls during surveys for spotted owls may be low and highly variable (Bailey et al.

Received: 3 May 2010; Accepted: 31 August 2010

¹E-mail: david.wiens@oregonstate.edu

2009). Nondetection of barred owls in areas co-occupied by spotted owls can have a sizeable influence on observed co-occurrence patterns, which, if not accounted for, could lead to weak or inaccurate inferences about the effects of barred owls on spotted owls.

Despite the need to more fully understand detectability and population trends of barred owls in forests managed for spotted owls, the costs associated with estimating these parameters over large areas may be prohibitively expensive when added to the already substantial costs associated with spotted owl research and management. Population assessments based on occupancy data may provide a cost effective alternative. Rather than focusing on uniquely identifiable individuals, the sampling methods outlined by MacKenzie et al. (2002, 2006) provide estimates of detection probability and the proportion of sampled area occupied by a species. In the case of barred owls, this approach may allow researchers to more accurately characterize presence over a wide range of spatial scales while providing the flexibility needed to account for potentially different (or changing) sources of variation in detectability and abundance. Nonetheless, the design of efficient survey strategies to reliably estimate barred owl presence will require careful consideration of response behavior and the factors affecting detectability.

We investigated response behavior, detection probabilities, and landscape occupancy patterns of barred owls in western Oregon, USA. We based our approach to locating and monitoring barred owls on repeated presence—absence surveys of randomly placed sampling units during the breeding season. We also surveyed spotted owls in our study area, which provided a unique opportunity to evaluate the response behavior and detectability of barred owls during conspecific versus spotted owl surveys. Thus, our specific objectives were to: 1) characterize response behavior, detectability, and landscape occupancy patterns of barred owls; 2) identify potential differences in response behavior of barred owls exposed to conspecific versus spotted owl vocalizations; and 3) provide recommendations to improve strategies for monitoring barred owls in the range of the spotted owl.

STUDY AREA

Located in the central Coast Range of western Oregon, the 745-km² study area included a mixed ownership of lands administered by the United States Bureau of Land Management (BLM, 48%), private timber companies (47%), Oregon Department of Forestry (ODF, 3%), and other private landowners (2%). Throughout the study area, square-mile sections of federal or state owned lands alternated with sections of privately owned lands to produce a checkerboard pattern of land ownership (Richardson 1980). Divergent forest management practices among public and private ownerships in the region have resulted in strong contrasts in forest conditions; whereas federal and state lands contained most mature and old forests, private lands managed for timber production were largely covered by young forests (<60 years old) and recent clear-cuts (Stanfield et al. 2002, Ohmann et al. 2007, Spies et al. 2007). Elevation ranged from 275 m to 2,300 m, with the terrain being highly dissected by steep slopes and a high density of streams. Forests of this region were dominated by Douglas-fir (Pseudotsuga menzeiesii), western hemlock (Tsuga herophylla), and western redcedar (Thuja plicata). Hardwoods, especially bigleaf maple (Acer macrophyllum) and red alder (Alnus rubra), occupied recently disturbed sites and riparian areas.

METHODS

Owl Surveys

Our sampling scheme for barred owls followed a standard occupancy design (MacKenzie et al. 2002, MacKenzie and Royle 2005) in which we surveyed randomly placed sampling units on multiple occasions regardless of their previous history of barred owl detections. We delineated sampling units by overlaying 149 equal-sized (500 ha) hexagonal cells on the study area. Within each cell, we placed calling stations 500-800 m apart along logging roads and forest trails to provide complete coverage of the study area. Sample unit size corresponded with mean home range sizes reported for barred owls in the Pacific Northwest (Hamer et al. 2007:762, Singleton et al. 2010:289). We selected this sampling scale because it encompassed a wide range of variability in home range sizes, which helped account for an unknown amount of spatial variation resulting from random placement of sampling units relative to actual

territory locations. We assumed that a detection of ≥ 1 barred owl during a survey indicated that some portion of the sampling unit was used by the owl(s) detected and that the size and distribution of actual territory locations did not change considerably during the breeding season. We conducted all surveys at night during 1 March-31 August 2009, allowing ≥2 days between each survey occasion. A combination of day and night visits is typically used to determine occupancy status for both owl species (Lint et al. 1999, U.S. Fish and Wildlife Service [USFWS] 2009). However, we only included night surveys in our analyses because this is when barred owls are most active and responsive to call-broadcast surveys (McGarigal and Fraser 1985), and our primary interest was in characterizing barred owl response behavior under optimal sampling conditions.

We followed a recently developed protocol to conduct surveys for barred owls (USFWS 2009) that included ≥3 nighttime surveys of each sampling unit. During each survey observers spent ≥15 min at established call stations alternately broadcasting barred owl vocalizations and listening for responses. We used an amplified megaphone (Wildlife Technologies, Manchester, NH) to broadcast digitally recorded barred owl calls, which included the single-note hoot, 2-phrase hoot, ascending hoot, and pair duet call (Mazur and James 2000, Odom and Mennill 2010). For each barred owl response we recorded sex (if known), pair status, response type (vocal with no approach or silent approach with or without vocalization), and time elapsed since the start of the broadcast. We identified the sex of vocal responses by the female's higher pitched calls and longer terminal notes (McGarigal and Fraser 1985, Mazur and James 2000, Odom and Mennill 2010). All observers were experienced owl biologists trained to recognize sex-specific differences in barred owl vocalizations. We considered an area to be occupied by a territorial pair of barred owls if we observed: 1) both sexes within 400 m of each other on ≥ 2 visits, 2) both sexes perched together at the same time, or 3) ≥1 adult with young (USFWS 2009). Single owls that we observed in the same general area on ≥ 2 visits were classified as single residents. Once we detected a pair of owls, we excluded all calling stations within an 800-m radius of the detection from the current survey (USFWS 2009). Survey exclusions were important in that they reduced the likelihood of detecting the same owls in adjacent sampling units on the same survey occasion. As part of a separate study of resource selection, we monitored 28 radio-marked barred owls at 21 territories during 2007-2009. We excluded the area within an 800-m radius of radio-marked owl activity centers from surveys to minimize disturbance to these owls. Nonetheless, information on the movements of marked individuals in the study population allowed us to more accurately distinguish among territories occupied by marked versus unmarked owls. We did not exclude areas known to be occupied by spotted owls from surveys for barred owls.

We surveyed spotted owls separately in 2009, which allowed us to evaluate the response behavior and detectability of barred owls during conspecific versus spotted owl survey

types. We followed a standardized survey protocol to locate and monitor spotted owls (Lint et al. 1999) that included ≥ 3 nighttime surveys of areas extending 2.0-2.5 km out from historically occupied spotted owl activity centers. During each survey observers spent ≥10 min at established call stations alternately listening for responses and broadcasting spotted owl calls. In 2009, we completed nighttime surveys of spotted owls at 30 historically occupied territories that completely overlapped 47 (32%) of 149 sampling units used to survey barred owls. Thus, we surveyed all 149 sampling units on 3 occasions using barred owl calls and 47 of these units an additional 3 times using spotted owl calls. Aside from the type of calls used to elicit responses, the most notable other difference between the 2 survey protocols was the minimum amount of time surveyors were required to spend at call points (10 min for spotted owl surveys versus 15 min for barred owl surveys). Surveyors generally adhered closely to these guidelines but often remained at call points for up to 30 min to determine pair status of single owl responses by listening for both sexes.

Data Analysis

We evaluated the response behavior of barred owls to callbroadcast surveys by estimating the number of owls detected per station surveyed (response rate) and the time elapsed between the start of the broadcast and a response (response time). To assess if response rate varied among breeding stages or monthly time intervals, we used a mixed model repeated measures analysis of variance with an autoregressive covariance matrix to adjust for repeated detections in sampling units (Littell et al. 1996). Here, we treated breeding stage or month as fixed effects and sampling unit as a random effect. We defined the transition between incubation (1 Mar-15 May), nestling (16 May-15 Jun), and fledgling-dependency (16 Jun-31 Aug) breeding stages using approximate mean dates (USFWS 2009). We used a contingency test of independence to examine potential differences in response rates between sexes and between conspecific and spotted owl surveys.

We used single-species, single-season occupancy models in Program MARK (White and Burnham 1999) to estimate the probability of detecting ≥ 1 barred owl at sampling unit i on occasion t, given presence (p), and the proportion of sampled area occupied by barred owls (ψ). We also calculated the overall probability of detecting ≥1 barred owl at least once during K surveys of an occupied sampling unit (p^*) as $1 - (1 - p)^K$ (MacKenzie and Royle 2005). Anticipating heterogeneity in parameter estimates and minimizing its effects—through both study design and by collecting relevant covariates to model existing variation—is essential for good performance of occupancy models (MacKenzie et al. 2006). Consequently, we developed a small set of a priori models to explain potential site- and survey-specific sources of variation in barred owl occupancy and detection probabilities. Our base model, $\{\psi(.) \ p(.)\}\$, assumed that these parameters were constant across sampling units and survey occasions, whereas model $\{\psi(.) p(t)\}$ allowed detection probabilities to vary across survey occasions. Calling behavior of barred owls, and thus the ability to detect barred owls during call-broadcast surveys, may vary seasonally depending on breeding stage (Mazur and James 2000). Moreover, barred owls may be less likely to respond to spotted owl calls than to conspecific calls (Gutiérrez et al. 2007). We therefore predicted that the probability of detecting barred owls would be most strongly influenced by breeding stage and survey type (conspecific vs. spotted owl), and modeled the direct effects of these time-varying covariates on estimates of p with the general form $\{\psi(.) \ p(\text{covariate})\}$. We expected the probability of detecting barred owls to be higher for conspecific than for spotted owl surveys and investigated how this effect varied with breeding stage by ranking models containing additive, $\{\psi(.) \ p(\text{stage} + \text{survey type})\}\$, and interactive, $\{\psi(.) \ p(\text{stage} \times \text{survey type})\}\$, effects. Survey effort for spotted and barred owls was not equal, so we coded spotted owl survey occasions for 102 (68%) of 149 sampling units as missing observations (MacKenzie et al. 2002, 2006).

Barred owls are typically associated with structurally complex mature and old forests (Hamer et al. 2007, Livezey 2007, Singleton et al. 2010). In our study area, these forest conditions were primarily limited to federal (BLM) and state (ODF) lands because private industrial lands, which comprised 47% of the study area, had been intensively managed for timber production and were mostly covered by earlysuccessional forests and recent clear-cuts. We therefore expected the variation in forest structural conditions associated with the checkerboard pattern of public and private lands in our study area to result in substantial variation among sampling units in the probability of occupancy. To account for this source of landscape heterogeneity in our analysis, we evaluated the proportion of public ownership within each sampling unit as a continuous, site-specific covariate relative to estimates of the proportion of sampled area occupied by barred owls. This single covariate allowed us to account for broad-scale differences in forest conditions among sampling units while minimizing model complexity and reducing unexplained heterogeneity in occupancy probabilities. We used a digitized cover map of land ownership (Oregon Geospatial Enterprise Office 2004) in ArcGIS version 9.3 to calculate land ownership proportions for each sampling unit. We did not evaluate the effect of land ownership on the probability of detection because we conducted all surveys at night with limited visibility. We estimated relationships between model parameters and covariates under the logistic model with a logit link function (MacKenzie et al. 2002), and determined the effects of covariates on the probability of detection and the proportion of area occupied by evaluating 95% confidence intervals of slope coefficients $(\hat{\beta})$ and the degree to which intervals overlapped zero. We ranked 11 candidate models using the second-order Akaike's Information Criterion (AIC_c) and evaluated the strength of evidence for each model using ΔAIC_c, Akaike weights, and evidence ratios (Burnham and Anderson 2002). We assessed model fit using a bootstrap estimate of the Pearson's chi-square statistic (MacKenzie and Bailey 2004).

Table 1. Sampling effort, detection probabilities, and total numbers of barred owls detected during conspecific versus spotted owl call-broadcast surveys conducted in western Oregon, USA, 2009.

Survey type and occasion	Units surveyed	Units with ≥1 detection	$\begin{array}{c} \textbf{Proportion of} \\ \textbf{units with} \geq \! 1 \ \textbf{detection}^{a} \end{array}$	Cumulative detection probability ^b	No. barred owls detected ^c
Barred owl					
Visit 1	149	86	0.58	0.66	149
Visit 2	149	85	0.57	0.88	150
Visit 3	149	90	0.60	0.96	145
Spotted owl					
Visit 1	45	22	0.49	0.48	37
Visit 2	47	23	0.49	0.73	37
Visit 3	45	17	0.38	0.86	35

^a We detected barred owls in 126 (85%) of 149 sampling units over all 6 visits combined.

RESULTS

Barred Owl Response Behavior

Over 3 conspecific survey occasions we detected 245 males, 187 females, and 12 non-juvenile barred owls of undetermined sex at 1,808 call stations (745 km²), resulting in an overall mean of 24.6 owls detected per 100 stations surveyed (0.60 owls detected/km²). There was little variability in total numbers of barred owls detected in the study area on each survey occasion ($\overline{x} = 148.0$, SD = 2.7, range = 145– 150 owls, Table 1). Based on the criteria we used to determine an owl's social status, responses were from as many as 61 territorial pairs, 3 resident single owls (all males), and 25 owls for which we were unable to determine pair status. These estimates do not include an additional 21 territorial pairs that we excluded from surveys. Overall response rate $(\bar{x} \pm SE)$ was higher for males (13.6 \pm 0.8) than females $(10.2 \pm 0.7, \chi^2 = 8.84, P = 0.003)$, but response rate did not vary among breeding stages for either sex (M: $F_{2,300} = 0.60$, P = 0.55; F: $F_{2,300} = 2.63$, P = 0.07). Response rates calculated at monthly intervals showed that we detected <5% of females (n = 9 of 187) during the early stages of egg laying (Fig. 1), but female response rate during this time did not deviate substantially from the overall mean

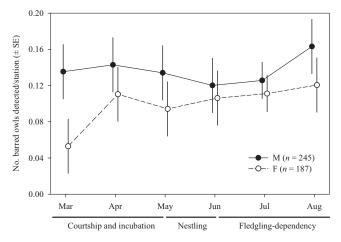
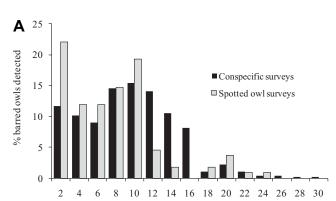


Figure 1. Monthly estimates of the number of male and female barred owls detected per call station during conspecific call-broadcast surveys conducted between 1 March and 31 August 2009, in western Oregon, USA.

 $(F_{2,300} = 2.42, P = 0.12)$. Response time to conspecific calls averaged 9.3 ± 0.3 min (range = 0–42 min, n = 444) and was similar for males $(9.1 \pm 0.4 \text{ min})$ and females $(9.6 \pm 0.4 \text{ min})$. Whereas most barred owls (90%) responded in ≤ 15 min, considerably fewer (61%) responded within the first 10 min of the sampling period (Fig. 2). Most barred owls (59%) responded vocally, but we initially detected 181 (41%) of 444 owls visually as they approached surveyors silently. We also detected 26 spotted owls (12 M, 14 F) during surveys for barred owls, which showed that spotted owls were somewhat responsive to barred owl calls.



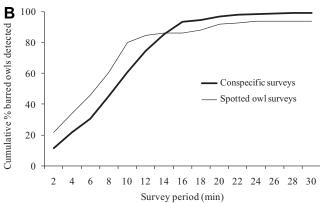


Figure 2. Percent (A) and cumulative percent (B) of barred owls detected within successive 2 min time intervals during conspecific versus spotted owl call-broadcast surveys conducted in western Oregon, USA, 2009. Minimum sampling period during conspecific and spotted owl surveys was 15 min and 10 min, respectively.

b Defined as the probability of detecting ≥ 1 barred owl at least once during K surveys of an occupied sampling unit; calculated as $1-(1-\hat{p})^K$, where $\hat{p}=$ the single visit detection probability estimated under the best-supported occupancy model.

^c Non-juvenile owls only. Estimates do not include an additional 21 territorial pairs we excluded from surveys.

Barred owls detected during surveys for spotted owls included 55 males, 37 females, and 17 individuals of undetermined sex at 736 call stations (327 km²), resulting in an overall mean of 14.8 owls detected per 100 stations surveyed (0.33 owls detected/km²). Overall response rate was $10 \pm 4\%$ lower for spotted owl surveys as compared to conspecific surveys ($\chi^2 = 32.59, P < 0.001$). Mean response time of barred owls to spotted owl calls (9.31 \pm 1.03 min, range = 0-51 min, n = 109) was nearly identical to that observed for conspecific calls. Eighty-seven (80%) of 109 barred owls responded within the 10-min sampling period specified by the spotted owl survey protocol, with 86% detected in ≤15 min (Fig. 2A,B). The percentage of barred owls we detected within the first 2 min of the sampling period was notably higher during surveys for spotted owls (22%) as compared to conspecific surveys (12%; Fig. 2A), and we detected more barred owls visually as they approached silently (62% vs. 40%, respectively).

Probability of Detection and Proportion of Area Occupied

We detected ≥1 barred owl in 126 (85%) of 149 sampling units surveyed 3-6 times during 1 March-31 August 2009 (Table 1). Mean number of non-juvenile barred owls detected in each 500 ha sampling unit was 1.0 (SE = 0.05, range = 0-4, n = 447). We found no evidence of lack of model fit based on the bootstrap results from our most highly parameterized model ($\chi^2 = 2074.57$, P = 0.43, $\hat{c} = 0.96$). Our best-fitting occupancy model, { ψ (ownership) p(survey type), contained 93% of the AIC, weight across the model set and was >23 times more likely than the next best model (Table 2). Consistent with our predictions, this model indicated that per-visit detection probabilities were higher for conspecific surveys ($\hat{p} = 0.66$, SE = 0.03, 95% CI = 0.61–0.71) than for spotted owl surveys ($\hat{p} = 0.48$, SE = 0.04, 95% CI = 0.39-0.56) and that occupancy was positively influenced by the amount of public ownership in the sampling unit ($\hat{\beta} = 4.67$, SE = 1.69, 95% CI = 1.36– 8.00). Using single-visit estimates of detection probability from the best-supported model, the overall probability of detecting ≥1 barred owl at least once during 3 nighttime surveys of an occupied sampling unit (p^*) was 0.96 for

conspecific surveys and 0.86 for spotted owl surveys (Table 1). Models that did not include effects of survey type or land ownership were not supported by the data (AIC_c wt = 0.0, Table 2). Moreover, we found no evidence of time dependency in detection probabilities as shown by a lack of support for models containing the effects of survey occasion (t) or breeding stage. The model-averaged occupancy estimate ($\hat{\psi} = 0.89$, SE = 0.03, 95% CI = 0.80–0.93) was only 4% higher than the naïve estimate (0.85), which reflected a high likelihood of detecting territorial barred owls over multiple visits.

DISCUSSION

When combined with a standardized survey protocol (USFWS 2009) and the analytical framework of MacKenzie et al. (2002, 2006), our sampling design was highly effective in estimating the distribution and landscape occupancy patterns of barred owls while accounting for imperfect detection. Barred owls are strongly territorial and highly responsive to conspecific calls (McGarigal and Fraser 1985), but our finding that single visit detection probabilities were <1 indicates that multiple surveys are required to maximize the likelihood of detecting barred owls that are present. In our study, 3 nighttime surveys conducted between the incubation and fledgling-dependency periods resulted in an overall detection rate of >95%. We also found that response behavior and detection probabilities of barred owls varied between spotted owl and conspecific surveys, which indicates that barred owl occurrence is higher than what is generally recognized by spotted owl monitoring programs. These results emphasize the need to account for erratic response behaviors that can lead to reduced or variable detection of barred owls during call-broadcast surveys.

Barred Owl Response Behavior and Detection Probabilities

We were unable to assess the response behavior and detectability of barred owls prior to nesting, but we found little evidence that seasonal changes in breeding behavior led to substantial variation in detection probability during the breeding season. There was some evidence, however, that

Table 2. Ranking of single-season occupancy models used to examine variation in the probability of detection (p) and proportion of area occupied (ψ) for barred owls in western Oregon, USA, 2009.

Model ^a	No. parameters	AIC, b	ΔAIC, b	AIC, wtb	Deviance
$\{\psi(\text{ownership}) \ p(\text{survey type})\}$	4	776.28	0.00	0.93	768.00
$\{\psi(.) \ p(\text{survey type})\}$	3	782.48	6.20	0.04	776.32
$\{\psi(.)\ p(\text{stage} + \text{survey type})\}$	4	783.70	7.42	0.02	775.42
$\{\psi(\text{ownership}) \ p(.)\}$	3	787.86	11.58	0.00	781.69
$\{\psi(.) \ p(\text{stage} \times \text{survey type})\}$	14	788.86	12.42	0.00	757.56
$\{\psi(.) \ p(t + \text{survey type})\}$	8	789.03	12.75	0.00	772.00
$\{\psi(.) \ p(.)\}$	2	793.14	16.86	0.00	789.06
$\{\psi(.) \ p(t \times \text{survey type})\}\$	13	794.03	17.75	0.00	765.33
$\{\psi(.)\ p(\text{stage})\}$	3	794.86	18.58	0.00	788.69
$\{\psi(.)\ p(t+\text{stage})\}$	8	797.70	21.42	0.00	780.67
$\{\psi(.)\ p(t)\}$	7	799.72	23.44	0.00	784.92

^a Time effects modeled as constant (.) or varying with survey occasion (*t*). Model covariates include breeding stage (incubation, nestling, fledgling-dependency), survey type (conspecific, spotted owl), and land ownership (proportion of sampling unit with federal or state ownership).

 $^{^{\}circ}$ AIC_c = Akaike's Information Criterion adjusted for small sample size, Δ AIC_c = difference between the AIC_c value of each model and the lowest AIC_c model, AIC_c wt = Akaike weight.

females were less responsive during the early stages of egglaying as we detected 6-10% fewer females in March as compared to all other months of the breeding season. Response rates of males were consistently higher than those for females and varied little over time. The sex-specific differences we observed in response behavior were most likely driven by differences among individuals in nesting and territorial status, but this level of individual variation could not be accommodated in our analyses. Based on vocal responses we were able to putatively distinguish among males and females, and we assumed that these decisions were valid for our analyses. Although some unknown level of identification error was likely, we believe such errors were rare because most (75-82%) vocal responses were from territorial pairs and previous studies have shown that the sex of barred owls can be reliably classified in the field based solely on their calls (Odom and Mennill 2010).

Barred owls responded throughout the 15-min sampling period specified by the survey protocol for this species (USFWS 2009), with 90% of all responsive owls detected in \leq 15 min. Similar to the observations of Smith (1975) and McGarigal and Fraser (1985), we observed a variety of response behaviors to conspecific calls; many owls approached surveyors quickly and quietly, whereas others responded vocally throughout the survey period from a range of distances (0–1.5 km). Vocal responses included \geq 10 different vocalizations described elsewhere (Mazur and James 2000, Odom and Mennill 2010), but most often included the 2-phrase hoot, ascending hoot, and pair duet call. Agitated barred owls were often heard crashing through the branches of the lower forest canopy as they approached surveyors, which we believe is a form of agonistic behavior used to intimidate intruders. In cases where surveyors heard branch-crashing but were unable to confirm presence of a barred owl, we found that broadcasting the pair duet call would often increase the owl's agitation level to the point where it would either vocalize or move in close enough to be seen. We did not use this method during surveys for spotted owls.

Probability of detecting ≥1 barred owl during one visit to an occupied sampling unit (0.66) was comparable to that estimated for several other forest owl species (range = 0.13-0.76; Flesch and Steidl 2006), including spotted owls (range = 0.53-0.76; Reid et al. 1999, Olson et al. 2005). Our study was limited in that it was based on 1 year of data, so we were unable to investigate potential annual variation in detection probabilities. We also did not explore several other potentially important sources of variation in detectability such as pair and reproductive status of individuals, distance to nests, time of day, or time of year (other than the breeding season), which were beyond the scope of our study. Moreover, our survey methods were directed towards eliciting responses from territorial individuals, so detectability may be different from that of unpaired or non-territorial individuals. Although including these various factors in our analyses may have explained additional variation in the data, model selection results from our occupancy analysis demonstrated that much of the heterogeneity in detection and

occupancy parameters was explained by the type of survey used to detect barred owls and the land ownership conditions within sampling units.

Detectability of Barred Owls During Surveys for Spotted Owls

Not surprisingly, our analyses provided evidence that response behavior and detection probabilities of barred owls varied with survey type. On average, response rates of barred owls were 10% lower and single visit detection probabilities were 18% lower during surveys for spotted owls as compared to conspecific surveys. Our estimate of detection probability for barred owls during nighttime surveys for spotted owls (0.49) was consistent with those reported from elsewhere in western Oregon (0.42-0.43, Bailey et al. 2009). These estimates suggest that one night visit using spotted owl calls will miss the presence of ≥ 1 barred owl about half the time, whereas one night visit using barred owl calls would only miss the presence of barred owls about a third of the time. Thus, on a per-visit basis, the low detection probabilities for barred owls during surveys for spotted owls can be expected to result in large discrepancies between naïve and estimated occupancy probabilities. With as many as 3 nighttime surveys for spotted owls, however, these discrepancies diminished and the overall probability of detecting barred owls that were present was reasonably high (0.86).

Barred owls appeared to exhibit a different behavioral response to spotted owl versus conspecific vocalizations, as shown by the higher prevalence of silent approaches during surveys for spotted owls. Aside from the type of calls used to elicit responses, other procedural differences between spotted and barred owl survey protocols may have also contributed to survey-specific variation in detection probabilities. In particular, the shorter survey period used during surveys for spotted owls may have limited our ability to detect barred owls that responded late in the survey period. This limitation was highlighted by a marked difference between survey types in the percentage of barred owls detected between 10 min and 15 min of the survey period (31% for conspecific surveys vs. 6% for spotted owl surveys). Collectively, these findings suggest that differences in the response behavior of barred owls exposed to conspecific versus spotted owl vocalizations in combination with a shorter survey period may have reduced the likelihood of detecting barred owls that were present during nighttime surveys of spotted owls.

Our finding that detection probabilities of barred owls varied with survey type supports many of the concerns surrounding the reliability of barred owl data collected incidentally to spotted owl research (Gutiérrez et al. 2007, Livezey and Flemming 2007, Bailey et al. 2009). The most obvious way to increase detectability of barred owls relative to spotted owl research is to survey directly for barred owls using conspecific calls, which increased single visit detection probabilities in our study by 13–32%. We caution, however, that this approach may be problematic because using barred owl calls in areas co-occupied by spotted owls might have the counteractive effect of reducing responsiveness of spotted owls (Crozier et al. 2006). Despite this concern, however, it

is important to recognize that survey effort for spotted owls is a function of detection, where little or no survey effort is required in areas where spotted owls are quickly located during daytime visits to active nesting areas (Franklin et al. 1996, Lint et al. 1999). This aspect of spotted owl monitoring programs could easily result in the non-detection of spatially associated barred owls, particularly in years of good spotted owl reproduction (Livezey and Flemming 2007). Identifying areas that may be co-occupied by both species is perhaps one of the most important, yet elusive aspects of evaluating the competitive effects of barred owls on spotted owls. Consequently, we suggest that carefully designed species-specific surveys will provide the most reliable baseline information required for assessments of the interspecific relationship between the 2 species. Species-specific surveys should be separated sufficiently in time to avoid exacerbating potential negative interactions between the species.

Occupancy, Distribution, and Abundance of Barred Owls

Overall occupancy probability of barred owls in an intensively managed forest landscape in western Oregon was high (0.89), which reflected a dramatic increase in barred owl occurrence in the region over the past 3 decades (Taylor and Forsman 1976). Barred owls were non-randomly distributed in our study area, with occupancy being highest in sampling units that contained a high proportion of public ownership. This was not unexpected because forest cover and diversity are strongly correlated with land ownership patterns in the Oregon Coast Range (Stanfield et al. 2002, Ohmann et al. 2007, Spies et al. 2007), and the disparity in forest structures and ages among land ownerships was particularly evident in our study area where most private lands were dominated by early-successional forests and recent clear-cuts. Our use of land ownership as a course-scale surrogate for forest conditions probably missed many of the fine-scale forest characteristics that influence occupancy, but the strong support for this effect in our analysis clearly demonstrated that occupancy probabilities were greatest in the structurally diverse mature and old forests that occurred almost entirely on public lands. This finding is consistent with previous evaluations of landscape-scale habitat associations of barred owls in the Pacific Northwest (Hamer et al. 2007, Livezey 2007, Singleton et al. 2010) and is analogous the results of Spies et al. (2007), who reported that federal lands contained most current and future habitat for spotted owls in the Oregon Coast Range.

Our sampling design was not based on known territory locations, so actual barred owl home ranges probably overlapped >1 sampling unit. This form of non-systematic movement among sampling units does not overly affect model parameters, but in some cases the interpretation of the parameters are altered such that occupancy should now be interpreted as use (MacKenzie and Nichols 2004). For rare species with large home ranges relative to the size of sampling units, the proportion of area used will be considerably larger than the proportion of area where the species physically occurs (MacKenzie and Royle 2005). We believe

this difference was minimal in our study because: 1) we used an appropriately sized sampling unit that allowed for variation in barred owl space use, 2) our field methods minimized the likelihood of detecting the same individuals in >1 sampling unit on the same survey occasion, and 3) a high proportion of the barred owl study population was marked, allowing us to distinguish among territories occupied by marked versus unmarked individuals. We also found little variation among survey occasions in the total number of barred owls detected or in the number of sampling units where we detected >1 barred owl. Thus, although we did not evaluate how well our estimates of the proportion of area occupied corresponded with actual population size, our sampling methods did result in high detectability and constancy in the total numbers of barred owls detected per visit.

MANAGEMENT IMPLICATIONS

As a generalist predator and fiercely territorial invader, barred owls at high densities have the potential to affect a variety of native wildlife through competition, niche displacement, and predation. These impacts may be especially problematic for the conservation and recovery of spotted owls, as land managers will become increasingly challenged by the objectives of preserving the unique structural diversity of spotted owl habitat while attempting to account for the potentially overriding effects of a widespread competitor. Our findings suggest that species-specific surveys will provide the most reliable baseline information required for proposed research and management strategies to address the potential negative impacts of barred owls on spotted owls (Buchanan et al. 2007). If the primary objective is to locate all territorial barred owls in a given area with high confidence, we recommend using 3 nighttime surveys with conspecific calls during the incubation, nestling, and fledgling-dependency periods (Feb-Aug). Because barred owls often approach surveyors quickly and silently, we recommend alternating broadcast and listening periods every 30-50 s and listening during the last 2–3 min of the survey period while visually searching the surrounding vegetation for owls that may have flown in silently. To increase detectability of barred owls during surveys for spotted owls, we recommend extending the survey period to >15 min and training observers to recognize the full repertoire of barred owl vocalizations. Researchers should also be aware that barred owls exhibit a diversity of response behaviors that can include rapid, silent approaches within the first several minutes of the sampling period in addition to distant, single-note vocal responses.

ACKNOWLEDGMENTS

We are indebted to R. Leach, P. Kolar, K. Skybak, A. Pantovich, S. Graham, J. Swingle, and J. Crawford for their field assistance. Funding was provided by the combined contributions of United States Geological Survey (Forest and Rangeland Ecosystem Science Center), USFWS, National Park Service, ODF, United States Forest Service (Pacific Northwest Research Station), and BLM. J. Thrailkill and members of the USFWS Barred Owl Survey Protocol group provided helpful guidance on

implementing surveys. We thank D. Barrett and T. Snetsinger for contributing spotted owl survey data, and Roseburg Forest Products, Weyerhaeuser Company, and Plum Creek Timber Company for providing access to their lands. B. Noon, K. Dugger, K. McKelvey, and 2 anonymous reviewers provided helpful comments and suggestions that improved our manuscript.

LITERATURE CITED

- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. S. Sovern. 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs 163.
- Bailey, L. L., J. A. Reid, E. D. Forsman, and J. D. Nichols. 2009. Modeling co-occurrence of northern spotted owls and barred owls: accounting for detection probability differences. Biological Conservation 142: 2983–2989.
- Buchanan, J. B., R. J. Gutiérrez, R. G. Anthony, T. Cullinan, L. V. Diller, E. D. Forsman, and A. B. Franklin. 2007. Research and management options to address potential competitive interactions between barred owls (*Strix varia*) and spotted owls (*S. occidentalis*). Biological Invasions 9:679–691.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, New York, USA.
- Crozier, M. L., M. E. Seamans, R. J. Gutiérrez, P. J. Loschl, R. B. Horn, S. G. Sovern, and E. D. Forsman. 2006. Does the presence of barred owls suppress the calling behavior of spotted owls? Condor 108:760–769.
- Dunbar, D. L., B. R. Booth, E. D. Forsman, A. E. Hetherington, and D. J. Wilson. 1991. Status of the spotted owl, Strix occidentalis, and barred owl, S. varia, in Southwestern British Columbia. The Canadian Field Naturalist 105:464–468.
- Flesch, A. D., and R. J. Steidl. 2006. Detectability and response rates of Ferruginous Pygmy owls. Journal of Wildlife Management 71:981–990.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology 17:12–20.
- Gutiérrez, R. M., M. Cody, S. Courtney, and A. B. Franklin. 2007. The invasion of barred owls and its potential effect on spotted owls: a conservation conundrum. Biological Invasions 9:181–196.
- Hamer, T. E., E. D. Forsman, and E. M. Glenn. 2007. Home range attributes and habitat selection of barred owls and spotted owls in an area of sympatry. Condor 109:750–768.
- Kelly, E. G., E. D. Forsman, and R. G. Anthony. 2003. Are barred owls displacing spotted owls? Condor 105:45–53.
- Leskiw, T., and R. J. Gutiérrez. 1998. Possible predation of a spotted owl by a barred owl. Western Birds 29:225–226.
- Lint, J. B., B. R. Noon, R. G. Anthony, E. D. Forsman, M. G. Raphael, M. Collopy, and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the northwest forest plan. General Technical Report PNW-GTR-440. U.S. Forest Service, Pacific, Northwest Research Station, Portland, Oregon, USA.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS systems for mixed models. SAS Institute, Cary, North Carolina, IISA
- Livezey, K. B. 2007. Barred owl habitat and prey: a review and synthesis of the literature. Journal of Raptor Research 41:177–201.

- Livezey, K. B., and T. L. Flemming. 2007. Effects of barred owls on spotted owls: the need for more than incidental detections and correlational analyses. Journal of Raptor Research 41:319–325.
- Mackenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.
- MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27.1:461–467.
- Mackenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.
- MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Boston, Massachusetts, USA.
- Mazur, K. M., and P. C. James. 2000. Barred owl (*Strix varia*). in A. Poole and F. Gill, editors. The birds of North America, No. 508, The Academy of Natural Sciences and The American Ornithologist's Union, Washington, D.C., USA.
- McGarigal, K., and J. D. Fraser. 1985. Barred owl responses to recorded vocalizations. Condor 87:552–553.
- Odom, K. J., and D. J. Mennill. 2010. A quantitative description of the vocalizations and vocal activity of the Barred Owl. Condor 112:549–560.
- Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management 69:918–932.
- Ohmann, J. L., M. J. Gregory, and T. A. Spies. 2007. Influence of environment, disturbance, and ownership on forest vegetation of coastal Oregon. Ecological Applications 17:18–33.
- Reid, J. A., R. B. Horn, and E. D. Forsman. 1999. Detection rates of spotted owls based on acoustic-lure and live-lure surveys. Wildlife Society Bulletin 27:986–990.
- Richardson, E. 1980. BLM's billion-dollar checkerboard. Forest History Society, Santa Cruz, California, USA.
- Singleton, P. H., J. F. Lehmkuhl, W. L. Gaines, and S. A. Graham. 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. Journal of Wildlife Management 74:285–294.
- Smith, C. F. 1975. Distributional ecology of barred owls and great horned owls in relation to human disturbance. Thesis, University of Connecticut, Storrs, Connecticut, USA.
- Spies, T. A., B. C. McComb, R. S. H. Kennedy, M. T. McGrath, K. Olsen, and R. J. Pabst. 2007. Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. Ecological Applications 17:48–65.
- Stanfield, B. J., J. C. Bliss, and T. A. Spies. 2002. Land ownership and landscape structure: a spatial analysis of sixty-six Oregon (USA) Coast Range watersheds. Landscape Ecology 17:685–697.
- Taylor, A. L., and E. D. Forsman. 1976. Recent range extensions of the barred owl in western North America, including the first records in Oregon. Condor 78:560–561.
- U.S. Fish and Wildlife Service. 2009. Draft interim guidance for conducting barred owl surveys within the range of the northern spotted owl: for use in experimental removal studies and determining abundance. U.S. Department of Interior, Portland, Oregon, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimates from populations of marked animals. Bird Study 46S:120–138.

Associate Editor: Kevin McKelvey.